composition. *Corallium* and *Tubipora*, for example, are compact forms, with little organic matter; and they are lower in magnesia than the genera with horny, organic axes, such as appear at the end of the table. It is also noteworthy that the highest proportions of calcium phosphate are commonly found associated with high values for magnesia.

[1] Published by permission of the Director of the U. S. Geological Survey.

AN EXPERIMENTAL ANALYSIS OF THE ORIGIN AND RELATIONSHIP OF BLOOD CORPUSCLES AND THE LINING CELLS OF VESSELS

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Studies on the origin and development of the cellular elements of the blood and the so-called endothelial cells which line the blood vessels in the normal embryo are peculiarly difficult on account of the important rôle that wandering mesenchyme cells play in these processes. The problem is also further confused by the perplexing mixture of cells of different origin brought about by the early established circulation of the body fluids. The development of no other embryonic tissue is so disturbed by mechanical and physical conditions.

A study of living fish embryos with the high power microscope has made it possible to observe the behavior of the wandering cells and to follow them in their development. The disadvantages due to the intermixture of cells in the blood current have been overcome by the investigation of embryos in which a circulation of the blood is prevented from taking place.

When the eggs of the fish, Fundulus heteroclitus, are treated during early developmental stages with weak solutions of alcohol, the resulting embryos in many cases never establish a blood circulation. In other respects these embryos may be very nearly normal and the development and differentiation of their tissues and organs often proceed in the usual manner, though at a somewhat slower rate. The heart and chief vessels are formed and the blood cells arise and develop in a vigorous fashion. The heart pulsates rhythmically but is unable to propel the body fluid since its venous end does not connect with the yolk vessels. And in many cases its lumen is partially or completely obliterated by periblastic material and nuclei which seem to be sucked into the heart cavity from the surface of the yolk.

In these embryos without a circulation of the blood, one is enabled

to study the complete development of the different types of blood corpuscles in the particular regions in which they originate. There is no contamination of the products of a given region through the introduction of foreign cells normally carried in the blood stream.

The actual power to form blood cells possessed by the different organs and tissues may be determined in the experimental embryos having no blood circulation. And the true haematopoetic function is thus clearly contrasted with the ordinary reproduction or multiplication of blood cells which might take place within the tissue spaces of such organs in the normal embryo.

The debated question regarding the production of blood cells from those cells lining the blood vessel wall may be convincingly answered, at least for the species here studied.

The results and conclusions derived from these experiments may be summarized as follows:

1. The fish embryo is capable of living and developing in an almost normal fashion without a circulation of its blood; this fact was first recorded by J. Loeb in 1893, yet this is the initial study of blood and vessel formation in such embryos. Red blood cells may be seen to arise and differentiate in these living embryos in two definite localities; the one within the posterior body region, and the other the blood islands on the yolk.

The blood cells remain confined to their places of origin, yet they attain a typical red color and may persist in an apparently functional condition on the yolk-sac for as long as sixteen to twenty days. The normal embryo becomes free swimming at from twelve to fifteen days, but individuals without a circulation never hatch although they may often live for more than thirty days.

All recent investigators have claimed that there are no blood islands present on the bony fish yolk-sac. Yet the presence of such islands is readily demonstrated in living Fundulus embryos, in the normal as well as in those with no circulation.

2. The plasma or fluid in the embryos which fail to develop a circulation begins to collect at an early time in the body cavities. The pericardium becomes hugely distended with fluid, as well as the lateral coelomic spaces and the Kupffer's vesicle at the posterior end of the embryo. The great distension of the pericardium due to this fluid accumulation pushes the head end of the embryo unusually far away from the surface of the yolk. The heart is thus often stretched into a long straight tube or string leading from the ventral surface of the head through the great pericardial cavity to the anterior yolk surface.

No blood vessels, or very few if any, form on the extreme anterior portion of the yolk-sac, so that the venous end of the heart is never connected with veins. And the heart does not draw fluid into its cavity to be pumped away through the aorta. When the heart cavity does contain fluid it is unable to escape and small floating particles may often be observed rising and falling with the feeble pulsations.

3. The hearts in embryos without a circulation are lined with a definite endocardium, but the myocardium or muscle wall is poorly developed, sometimes consisting of only a single cell layer. Pigmented cells are not present in the wall of the normal heart, but in the experimental hearts these large chromatophores are invariably found. The cavity in many of the hearts is almost if not entirely obliterated by the presence of periblastic material and huge amorphous periblast nuclei.

The conus end of such hearts leads directly to a more or less closed ventral aorta. Portions of the aortic arches are seen as open spaces, and the dorsal aortae are almost invariably seen as typical spaces lined by characteristic embryonic endothelium.

A point of much importance is the fact, that *neither these hearts with their endothelial linings nor any portion of the aortae at any stage of development have ever been seen to contain any form of red blood corpuscle.* Cells of this type are completely absent from the anterior regions of the embryo.

4. Pigment cells normally occur on the Fundulus yolk-sac and arrange themselves along the vascular net so as to map out the yolk-sac vessels in a striking manner. Loeb has thought that this arrangement along the vessel walls was possibly due to the presence of oxygen carried by the corpuscles within the vessels. In the embryos without a yolk-sac circulation the pigment cells arise but rarely become fully expanded so that the usual long branched processes are represented only by short projections; the chromatophore consequently seems much smaller than usual.

The unexpanded pigment cells, however, wander over the yolk-sac and collect in numbers around the plasma filled spaces. The yolk surface of the pericardium and the periphery of the Kupffer's vesicle are often almost covered with pigment. The hearts are during early stages full of plasma and the pigment cells form a sheath around them, while such cells are never present on the normal hearts during the embryonic period.

These facts would seem to indicate that the plasma rather than the blood corpuscles contains the substance which attracts the chromatophores and initiates their arrangement along the normal vascular net of the yolk-sac.

5. A definite mass of cells characteristic of the fish embryo is located in the posterior half of the body between the notochord and the gut and extends well into the tail region. This so-called 'intermediate cell mass' is the intra-embryonic red blood cell anlage in many of the species.

The peripheral cells of the mass as claimed by Swaen and Brachet, or the mesenchyme about the mass, Sobotta, form a vascular endothelium which encloses the central early blood corpuscles. In individuals without a circulation the erythroblasts arise in a normal manner in this centrally located position and become erythrocytes or red blood corpuscles filled with haemoglobin. Typical vascular endothelium completely surrounds the erythrocytes which, instead of being swept away as usual by the circulating current, remain in their place of origin. All of the early blood forming cells of this intermediate mass give rise to red corpuscles and never to white blood cells.

6. Contrary to the opinion of most recent observers on blood development in Teleosts, the Fundulus embryos both with and without a circulation, possess blood islands on the posterior and ventral portions of the yolk-sac. These blood islands are formed by wandering mesenchymal cells which migrate out from the caudal region of the embryo. They represent all that remains on the yolk-sac of the peripheral mesoderm in the Teleosts and probably wander away from mesoderm related to that of the intermediate cell mass. The intermediate cell mass may possibly represent the bulk of the peripheral mesoderm which is here included within the embryonic body, while in other meroblastic eggs it is spread out posteriorly over the yolk. The only mesodermal elements of the yolk-sac in Fundulus are the independent wandering mesenchyme cells, some of which group themselves to form the blood islands, while others give rise to the yolk vessel endothelium, and still other wandering cells develop into the chromatophores.

7. The non-circulating red-blood corpuscles within the embryo remain in a fully developed condition for eight or ten days and then undergo degeneration. In an old embryo of sixteen days it is sometimes found that very few of the corpuscles in the intermediate mass are still present and these are degenerate. The vascular endothelium has been lost and numerous mesenchyme cells have wandered in to lie among the corpuscles.

On the yolk-sac the corpuscles no doubt have a better oxygen supply and here they maintain their color longer, but finally also present a degenerate appearance with small densely staining nuclei and cell bodies much reduced in size.

8. Vascular endothelium arises *in loco* in many parts of the embryonic body other than those localities in which blood cells form. The endothelium is in all cases utterly incapable of giving rise to any type of blood cell. This incapacity cannot be attributed to the abnormal condition of the embryo, since true blood cell anlagen in the same specimen produce blood corpuscles in abundance.

The lining of the vessel walls in the fish embryo has no blood forming function.

9. Neither lymphocytes nor other types of white blood corpuscles, have been found to arise in the yolk-sac blood islands, nor within the intermediate cell mass. The embryonic white blood cells are found most abundantly in the anterior body and head regions, and there occupy extra-vascular positions usually lying among the mesenchymal cells.

The sources of origin of the white and red blood corpuscles in Fundulus embryos are distinct, and these two different types of cells cannot be considered to have a monophyletic origin except in so far as both arise from mesenchymal cells.

The adult blood of Fundulus contains lymphocytes and several varieties of granular leucocytes.

10. There is evidence to indicate that definite environmental conditions are necessary for blood cell proliferation or multiplication. Blood cells do not normally divide when completely enclosed by vascular endothelium. This is the key to the shifting series of so-called haematopoetic organs found during embryonic development.

Erythroblasts, embryonic red blood corpuscles, lying about spaces unenclosed by vascular endothelium, proliferate steadily and give off their products into the space from which they find their way into the embryonic vessels. Should such an erythroblast be carried by the circulation to another unlined space, it may become arrested there and again undergo a series of divisions, giving rise to other erythroblasts. When, however, these spaces become lined by endothelium, the blood cell reproduction stops.

In most embryos the earliest blood cell formation occurs in the yolk-sac blood islands. The cells in these islands continue to divide until they become surrounded by endothelium, then the yolk-sac blood islands lose their haematopoetic function and become a vascular net through which the blood circulates. The liver now takes up the rôle of harboring dividing blood cells within its tissue spaces. When these spaces become vascularized by endothelium, here again the blood cells no longer multiply but merely circulate.

Finally, in the mammalian embryo, one organ after another ceases

to offer the necessary harbor for dividing blood cells, until the red bone marrow is the only tissue presenting the proper relationship of spaces and vessels, and here alone the erythropoetic function exists to supply the red blood cells for the entire body circulation. The red blood corpuscles are always produced so as to be delivered into the vessels and thus very soon occupy an intra-vascular position and cease to divide, while the white blood cells arise and remain for some time among the mesenchymal tissue cells in an extra-vascular position.

11. Lymphocytes and leucocytes, so-called white blood cells, along with the invertebrate amoebocytes, are all generalized more or less primitive wandering cells, and are almost universally distributed through out the metazoa.

Erythrocytes, red blood corpuscles, are very highly specialized cells with a peculiar oxygen carrying function, due to their haemoglobin content. In contrast to the universal distribution of the leucocytes, the erythrocytes, the red corpuscles, are only found in the vertebrate phylum and in a few of the higher invertebrate groups. Yet in these invertebrates the oxygen carrying blood cell never presents the typically uniform appearance of the vertebrate erythrocyte. The oxygen carrying function in many invertebrates is confined to the liquid plasma.

The typical vascular endothelial cell is widely distributed in the animal kingdom and appears to be a simple slightly modified mesenchymal cell.

These three very different types of cells all seem to arise from mesoderm—the mesenchyme. Yet the present investigation would indicate that each arises from a distinctly separate mesenchymal anlage. The erythrocyte, red cell, anlage is localized and perfectly consistent in the quality of its production. The lymphocyte and leucocyte, white cell, anlage is more diffusely arranged and not definitely localized in any particular cells group. The vascular endothelium appears to be formed *in loco* in almost all parts of the embryonic body, and its formation is absolutely independent of a circulating fluid or the presence of blood cells.

On the yolk-sac of Fundulus embryos one finds four distinctly different products, red blood corpuscles, endothelium, and two varieties of chromatophores, differentiating from the apparently similar wandering mesenchymal cells. The environment in which the four types differentiate is identical as far as is possible to determine, and the only explanation of their various modes of differentiation is that the original mesenchymal cells that wandered out were already of four potentially different classes. These differences in potentiality within the cells pro-

duced the four different types of structure in one and the same environment. The four types of cells are then in an embryological sense polyphyletic in origin.

Therefore, *vascular endothelium, erythrocytes and leucocytes, although all arise from mesenchyme, are really polyphyletic in origin; that is, each has a different mesenchymal anlage.* To make the meaning absolutely clear, we may consider the origin of the liver and pancreas cells a parallel case, both arise from endoderm but each is formed by a distinctly different endodermal anlage, and if one of these two anlagen is destroyed the other is powerless to replace its product.

A more complete account of this work, with a discussion of the literature bearing on the subject, appears in the September and November numbers of the *American Journal of Anatomy.*

NOTICES OF BIOGRAPHICAL MEMOIRS

The following biographical memoirs have been published by the Academy since the last notices of such memoirs appeared in the June number of the Proceedings.

HENRY MORTON (1836–1902). By EDWARD L. NICHOLS. *Biographical Memoirs of the National Academy,* vol. **8,** pp. 143–151.

This Memoir consists in a description of the life-work of Henry Morton. It includes an estimate of his personality by Mr. Thomas A. Janvier quoted from the Morton Memorial Volume published by the Alumni Association of the Stevens Institute of Technology of which Mr. Morton was the first president.

PETER LESLEY (1819–1903). By W. W. DAVIS. *Biographical Memoirs of the National Academy,* vol. **8,** pp. 155–240.

This Memoir discusses the life-work of Peter Lesley, under the headings: Ancestry; Boyhood; First Geological Work; Early Appalachian Study; Theology and Geology at Princeton; A Year Abroad; Preaching in Pennsylvania; Geological Work in Boston; Preaching in Milton; Engagement and Marriage; The Lyman Family; Peter and Susan Lesley; Married Life in Milton; Lesley's Hobby, "Arkism;" Return to Pennsylvania and Geology; Anti-Slavery Opinions; Professional Work, its Pleasures and Pains; "Coal and its Topography;" Catastrophic Views; Soil-Creep; Lesley as a Draftsman; Personal Opinions; The American Philosophical Society; The Iron Manufacturers' Guide; A Later Estimate of Rogers; Personal Items; Lowell Institute Lectures; Man's Origin and Destiny; Lesley as a Philologist; "Five Types of Earth Surface;" Two Years Abroad; More Personal Items; A Characteristic Incident; Theoretical Views in Professional Reports; The University of Pennsylvania; Proofreading; The "Second Survey;" The Drudgery of Survey Work; Distractions and Entertainments; The American Association; Trips to Europe; The Dictionary of Fossils; Summary of Pennsylvania Geology; Recognition; Lesley in his Old Age.

At the close the author of the Memoir presents a personal appreciation of Mr. Lesley.